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Spatial patterns of insect herbivory within a forest landscape: the role of soil type and forest stratum

Xinliang Shao[1,2], Qin Zhang[1] and Xitian Yang[2*]

Abstract

Background: Insect herbivory has profound impacts on ecosystem processes and services. Although many efforts have been made to recognize the main drivers of insect herbivory at different scales, the results are inconsistent. One likely reason is that studies have insufficiently captured the spatially heterogeneous factors such as soil type and forest stratum within the stand that may significantly affect insect herbivory. In particular, there is a lack of studies that address the detailed spatial patterns of insect herbivory which are influenced by these factors.

Methods: We measured the detailed spatial patterns of insect herbivory on cork oak (*Quercus variabilis* Bl.) in response to soil type (gravel soil and loam) and forest stratum (the upper, lower, and sapling stratum), and correlated these patterns with a set of influencing factors (litter coverage, coverage of shrubs and herbs, soil nutrients, soil moisture, and leaf traits) in a forest landscape.

Results: Generally, insect herbivory was spatially heterogeneous within stands. Herbivory was significantly lower in gravel soil areas than in loam soil areas and the highest herbivory occurred in the lower stratum. However, there were also 41 individual plots in which the highest herbivory occurred in the upper stratum and 29 plots in which the highest herbivory occurred in the sapling stratum. There were significant differences in soil nutrient and water status between soil types, but no significant differences in leaf traits. The effects of forest stratum on leaf traits were also inconsistent with those on insect herbivory.

Conclusions: Leaf traits may not be the main factors influencing insect herbivory in the field. Soil type may have major effects on herbivory patterns by influencing litter coverage while higher coverage of shrubs and herbs may reduce herbivory in the sapling stratum. These findings may advance our understanding of tree-herbivore interactions in real-world situations and have important implications for the sustainable management of forest ecosystems.

Keywords: Forest stratum, Heterogeneity, Insect herbivory, Leaf litter, Leaf traits, Soil nutrient, Soil type

Introduction

Insect herbivory has profound effects on ecosystem processes and services by influencing nutrient dynamics (Belovsky and Slade 2001; Frost and Hunter 2004, 2008; le Mellec et al. 2011; Maguire et al. 2015; Metcalfe et al. 2015), affecting the growth, survival, and reproduction

of trees (Crawley 1989; Hochwender et al. 2003; Zvereva et al. 2012), demographics and succession of forests (Crawley 1989; Huntly 1991; Barbosa et al. 2005; Karlsen et al. 2013), as well as plant community composition (Crawley 1989; Huntly 1991; Frost and Hunter 2008).

There has been a growing interest in recognizing the key drivers of insect herbivory (e.g. Rossetti et al. 2017; Castagneyrol et al. 2019; Valdés-Correcher et al. 2019). At the landscape scale, numerous studies have demonstrated that landscape context such as patch size,

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isolation/connectivity have significant effects on insect herbivory (Simonetti et al. 2007; De Carvalho Guimarães et al. 2014; Martinson et al. 2014; Lantschner and Corley 2015; Castagneyrol et al. 2019; Valdés-Correcher et al. 2019). However, the results of these studies are inconsistent and a recent meta-analysis based on 89 individual studies demonstrated that habitat fragmentation had no significant effects on insect herbivory (Rossetti et al. 2017).

At the stand scale, tree diversity has been recognized as an important driver of insect herbivory in forest ecosystems. Many studies have demonstrated that trees grown in monocultures tended to receive more insect herbivory than that associated with other tree species in mixtures (Vehviläinen et al. 2007; Castagneyrol et al. 2014). However, inconsistent results have also been reported that increased tree diversity can increase insect herbivory (Schuldt et al. 2010, 2015; Haase et al. 2015), decrease insect herbivory in certain stratum (Castagneyrol et al. 2019), or have no effects at all (Rosado-Sanchez et al. 2018).

These conflicting results imply that the heterogeneous environment within stands/patches might have considerable effects on insect herbivory. In fact, biotic and abiotic factors such as the radiation, humidity, temperature, wind, and litter as well as vegetation coverage and foliage quality and quantity could vary widely among different spatial locations within stands/patches (Ries et al. 2004; Gámez-Virués et al. 2010; Maguire et al. 2016; Rossetti et al. 2017; Castagneyrol et al. 2019). All of these factors may affect insect herbivory. For instance, many studies have correlated insect herbivory with morphological and functional leaf traits (e.g. toughness, nutrients, or defense compounds). Specific leaf area (SLA) is often considered as an indicator for leaf toughness, which may negatively influence leaf palatability for insect herbivores (Brunt et al. 2006; Zehnder et al. 2009; Stiegel et al. 2017). Higher leaf nitrogen may promote the growth, development, and fecundity of insect herbivores, and increase insect density (Cisneros and Godfrey 2001; Stiling and Moon 2004; Huberty and Denno 2006). In contrast, carbon content can negatively influence leaf palatability (Feeny 1970; Southwood et al. 1986; Schädler et al. 2003; Stiegel et al. 2017). The high content of phenolic compounds may deter insect feeding, reduce insect performance, herbivore densities, and species richness (Rossiter and Baldwin 1988; Forkner et al. 2004). In addition, studies have demonstrated that soil nutrient status can significantly influence leaf traits (Cipollini et al. 2002; Adamidis et al. 2014; Vergara-Gómez et al. 2019), and thus indirectly affect insect herbivory (e.g. Stiling and Moon 2004). As two important components of habitat structure, the vegetation coverage and litter may also have significant effects on insect

herbivory by influencing the niches for arthropods (Gámez-Virués et al. 2010).

Studies have shown that herbivory at the edges is often higher than in patch interiors due to the reduction in natural enemy populations and high-quality hosts at the edges (Coley et al. 1985; Meiners et al. 2000; Valladares et al. 2006; Urbas et al. 2007; De Carvalho Guimarães et al. 2014).

The changes in microclimate (Stiegel et al. 2017), leaf traits (Dudt and Shure 1994; Thomas et al. 2010; Stiegel et al. 2017), and predation pressure (Aikens et al. 2013) along vertical gradients in forest canopy can also affect the parallel herbivory pattern. Generally, decreased herbivory patterns from understory to upper stratum have been reported (e.g. Stiegel et al. 2017; Castagneyrol et al. 2019). Thus, understanding both the horizontal and vertical spatial patterns of herbivory within stands is essential for unraveling the mechanisms underlying the complex forces that drive insect herbivory in real-world situations.

From previous observation, we found that different soil types (i.e. gravel soil or loam) might exist within the stand. The litter coverage in loam areas is evidently higher than that in gravel soil areas while insect damage on oak in gravel soil areas appears less than that in loam areas. Therefore, we speculate that soil type may have important effects on insect herbivory. However, perhaps due to the irregular distribution of different soil types, few studies have paid attention to the relationship between soil types and insect herbivory within stands. Whether different soil types can influence insect herbivory by differentially holding leaf litter which may provide shelter for the overwintering insect herbivores, or whether different soil types have contrast soil conditions and thus influence insect herbivory by affecting leaf traits are still unclear. In addition, although the effects of forest stratum on insect herbivory have been examined in studies involving different forests (e.g. European beech, *Fagus sylvatica* L. or sugar maple, *Acer saccharum* Marsh.) (Fortin and Mauffette 2002; Stiegel et al. 2017), little such knowledge is known about the cork oak (*Quercus variabilis* Bl.) forest. Furthermore, previous studies that investigated the spatial patterns of insect herbivory often sampled just a few tree individuals (e.g. 2 or 6) to represent the stand level (e.g. Stiegel et al. 2017; Castagneyrol et al. 2019) or location level (edge vs. interior) within the patch (e.g. Maguire et al. 2016), which may miss some spatial pattern effects or provide biased results. Detailed, fine-grained research involving relatively large numbers of sampling sites within stands is therefore required.

In the present study, we measured the detailed spatial patterns of insect herbivory on cork oak (*Quercus variabilis* Bl.) within a forest landscape and mainly focused

on the effects of soil type and forest stratum on insect herbivory. We also associated the spatial patterns with litter coverage, coverage of shrubs and herbs, soil nutrients (available N, P, K), soil moisture, and leaf traits (specific leaf area, tannin content, soluble sugar content, C content, N content, and C/N ratio) as well as the holding effects of different soil types on withered leaves and discussed the potential mechanisms. We predicted that (i) insect herbivory in gravel soil areas would be lower than that in loam areas; (ii) there would be a generally decreased pattern of insect herbivory from understory to upper stratum; (iii) the spatial patterns of insect herbivory might significantly correlate with litter, coverage of shrubs and herbs, soil conditions and leaf traits. By revealing the detailed spatial patterns of insect herbivory within a landscape and exploring the underlying mechanisms that drive these patterns in real-world situations, our study will offer insights for future studies on tree-herbivore interactions and have important implications for sustainable management of forests.

Materials and methods
Study area
The study was carried out in the west of Dengfeng City, Henan Province, China (34°26′–34°33′ N, 112°44′–113°5′ E). This region is covered by extensive plantations of cork oak (*Quercus variabilis* Bl.) and some of them contain cypress (*Platycladus orientalis* (L.) Franco), oriental white oak (*Quercus aliena* Bl.), and other tree species in minor abundance.
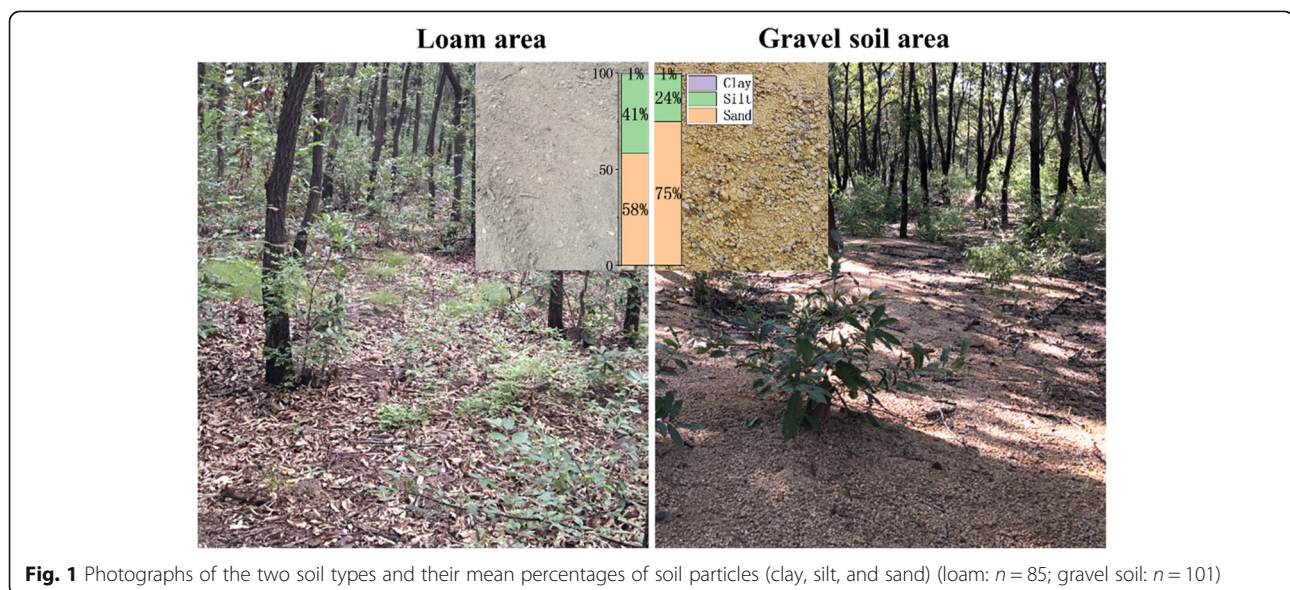
The main insect herbivores on cork oak trees are *Culcula panterinaria* (Bremer et Grey) (Lepidoptera, Geometridae) and *Phalera assimilis* (Bremer et Grey) (Lepidoptera, Notodontidae). Both of them are univoltine defoliators

(chewers). Their larvae begin to hatch in July and the mature larvae burrow into the soil and pupate for overwintering in September. Based on the satellite image and ground survey, we chose a ca. 200 ha area that was located on the south side of Songshan Mountain for study. We set a 10 m × 10 m plot every 100 m within the area beyond road landscapes and there were 186 plots in total (85 in loam areas, 101 in gravel soil areas). The elevation of these plots varied from 518 to 755 m.

Field investigation and laboratory measurement
The field investigation and leaf measurement were taken in late September 2019. In each plot, litter coverage, coverage of shrubs and herbs were measured. The soil was roughly classified into loam and gravel soil and it was easy to distinguish the soil type by visual judgment (Fig. 1). In each plot, we collected the top 10-cm soil at three random locations and pooled them together as one sample. After the measurement of soil moisture content, all soil samples were air-dried and sieved through a 2-mm mesh. Soil particle-size was determined using Mastersizer 2000 Particle Analyzer (Malvern Panalytical Ltd, Malvern, UK).

We randomly selected individual oak trees in each plot for leaf sampling. The oak tree canopies were divided into three strata in relative terms: the upper stratum, the lower stratum, and the sapling stratum. Thirty mature leaves were haphazardly collected per stratum. For the sapling stratum, leaves from at least 6 saplings were collected by hand. For the upper and lower strata, leaves from at least 3 trees were collected using a 10-m telescopic pole pruner. The leaves collected were stored in zipped plastic bags and put into a cool box immediately.

Fig. 1 Photographs of the two soil types and their mean percentages of soil particles (clay, silt, and sand) (loam: *n* = 85; gravel soil: *n* = 101)

Herbivory was measured in the laboratory. We only estimated the damages caused by chewers since other feeding guilds caused too scant damages for independent analyses. To improve the accuracy of the estimate, we overlaid the leaves on a sheet of blank paper printed with a grid of 0.25 cm^2 (0.5 cm × 0.5 cm). We calculated the total leaf missing area divided by the number of leaves analyzed (Castagneyrol et al. 2019).

To further investigate whether the spatial patterns of insect herbivory correlate with soil conditions and leaf traits, we examined soil moisture content and available N, P, and K across 186 plots and randomly selected 6 plots in loam and gravel soil areas respectively to examine the leaf traits including specific leaf area (SLA), tannin content, soluble sugar content, C content, N content in three strata. Soil conditions were measured according to Bao (2000). SLA was measured on 6 mature, fully expanded, and undamaged leaves. Leaf surface and leaf mass were measured with a planimeter (CL-203 Laser Area Meter, Bio-Science Inc., USA) and a balance (JEA3002 Electronic Balance, Shanghai Puchun Metrical Instrument Co., Ltd., China). Tannin content was measured using the ND-1-Y kit (Suzhou Keming Biological Technology Co. LTD). Soluble sugar content was measured using the KT-1-Y kit (Suzhou Keming Biological Technology Co. LTD). The procedures were performed as described by the manufacturer. The leaf C and N contents were determined using an elemental analyzer (HEKAtech GmbH, Wegberg, Germany; Euro EA 3000).

We investigated the overwintering pupae of main insect herbivores in November 2019. Since the density of overwintering pupae may be very low at the background level of insect herbivory, we randomly set three 15 m × 15 m plots on each type of soil (loam or gravel soil) and investigated the entire area in each plot (different from investigating a small area around the base of tree trunk (e.g. radius 100 cm)). We carefully pushed aside the litter and dug the top 10-cm soil to check the number of overwintering pupae and the location of the overwintering pupae inhabit (the litter, the soil under litter, or the bare soil).

The holding effects of soil on withered leaves were tested on loam and gravel soil respectively. We randomly selected 10 withered leaves and put them in a 20 cm × 20 cm area on the ground (loam or gravel soil) with no slope, then we used an electric fan to blow these withered leaves for 10 s (all leaves stopped moving within this time range) and measured the distance between the front edge of the small area and withered leaves that were blown away. The average moved distance per leaf indicated the holding effects of each soil on withered leaves. The shorter the distance, the stronger the holding effect. The annual mean wind speed is 3 m·s^{-1} in Dengfeng City (according to the data of the local meteorological station). Although

the wind speed may fluctuate, it can be effectively slowed down by tree canopy in the forest and decreases as the height decreases (Lee and Black 1993; Zhu et al. 2004; Ma et al. 2009; Randlkofer et al. 2010). We therefore used a small portable electric fan with three wind speeds (1.5, 2.5 and 4 m·s^{-1}) and did 6 replications at each wind speed on loam and gravel soil respectively.

Statistical analyses

We applied a linear mixed-effect model (LMM) to analyze the effects of soil type (loam vs. gravel soil) and forest stratum (upper, lower, and sapling) on insect herbivory (186 plots). Soil type, forest stratum, and soil type × forest stratum were included as fixed effects and the identity of study plots as a random factor. We used t-test to compare the difference of coverage of shrubs and herbs between plots that had the highest herbivory in the sapling stratum and plots that had the highest herbivory in the upper or lower stratum. The difference of coverage of shrubs and herbs, litter coverage, percentages of soil particles, and soil nutrients between soil types as well as holding effects of different soil types on withered leaves were analyzed with t-test. Significant interactions between soil type and stratum were treated by estimating contrasts between loam and gravel soil areas for each stratum separately and contrasts among strata for each soil type independently. The relationship between insect herbivory and the coverage of shrubs and herbs was determined by regression analysis. To test the effects of soil type and forest stratum on leaf traits (SLA, tannin content, soluble sugar content, N content, C content), we built another set of LMM (there were 6 plots in loam and gravel soil areas respectively) where the fixed effects and random factor were the same as the first LMM. All analyses were conducted using IBM SPSS Statistics 20 (SPSS Inc, Chicago, IL, USA) and the graphs were plotted using Origin 2018 (OriginLab, Northampton, MA, USA).

Geostatistical analysis

The spatial variability of insect herbivory was determined by geostatistical methods using semivariogram analysis. The semivariogram was calculated for each variable as follows:

$$r(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2 \tag{1}$$

where, $r(h)$ is the sample semivariance for the distance lag h, $Z(x_i)$ and $Z(x_i + h)$ are sample values at two points separated by the distance interval h, and $N(h)$ is the total number of sample pairs for the lag interval h. The sample semivariogram was calculated and the best geostatistical model for each parameter was chosen according to

the lowest residual sum of squares and the highest r^2 values. Spatial dependence of insect herbivory can be evaluated according to Cambardella et al. (1994). If the nugget to sill ratio $C_0/(C + C_0)$ is > 0.75, the herbivory is thought as weakly spatially dependent; if $C_0/(C + C_0)$ is between 0.25 and 0.75, the herbivory is considered moderately spatially dependent; and if $C_0/(C + C_0)$ is < 0.25, the herbivory is regarded to be strongly spatially dependent (Cambardella et al. 1994). If the distribution distances of sampling points are less than the spatial variation range (A), the variable of these points are spatially correlated; if the distances are greater than the range, the variable of these points are independent (Cambardella et al. 1994). The geostatistical analysis was performed using GS + 7.0 (Robertson 2008).

Results

Spatial heterogeneity of insect herbivory

Soil type and forest stratum had significant effects on insect herbivory (soil type: $F_{(1, 184)} = 70.05$, $P < 0.001$; stratum: $F_{(2, 368)} = 34.14$, $P < 0.001$; soil type × stratum: $F_{(2, 368)} = 11.10$, $P < 0.001$). Horizontally, the herbivory of three strata in loam areas was significantly higher than that in gravel soil areas (Figs. 2 and 3). In loam areas, herbivory in the lower stratum was significantly higher than that in the upper and sapling stratum and herbivory in the sapling stratum was significantly lower than that in the upper stratum (Figs. 2
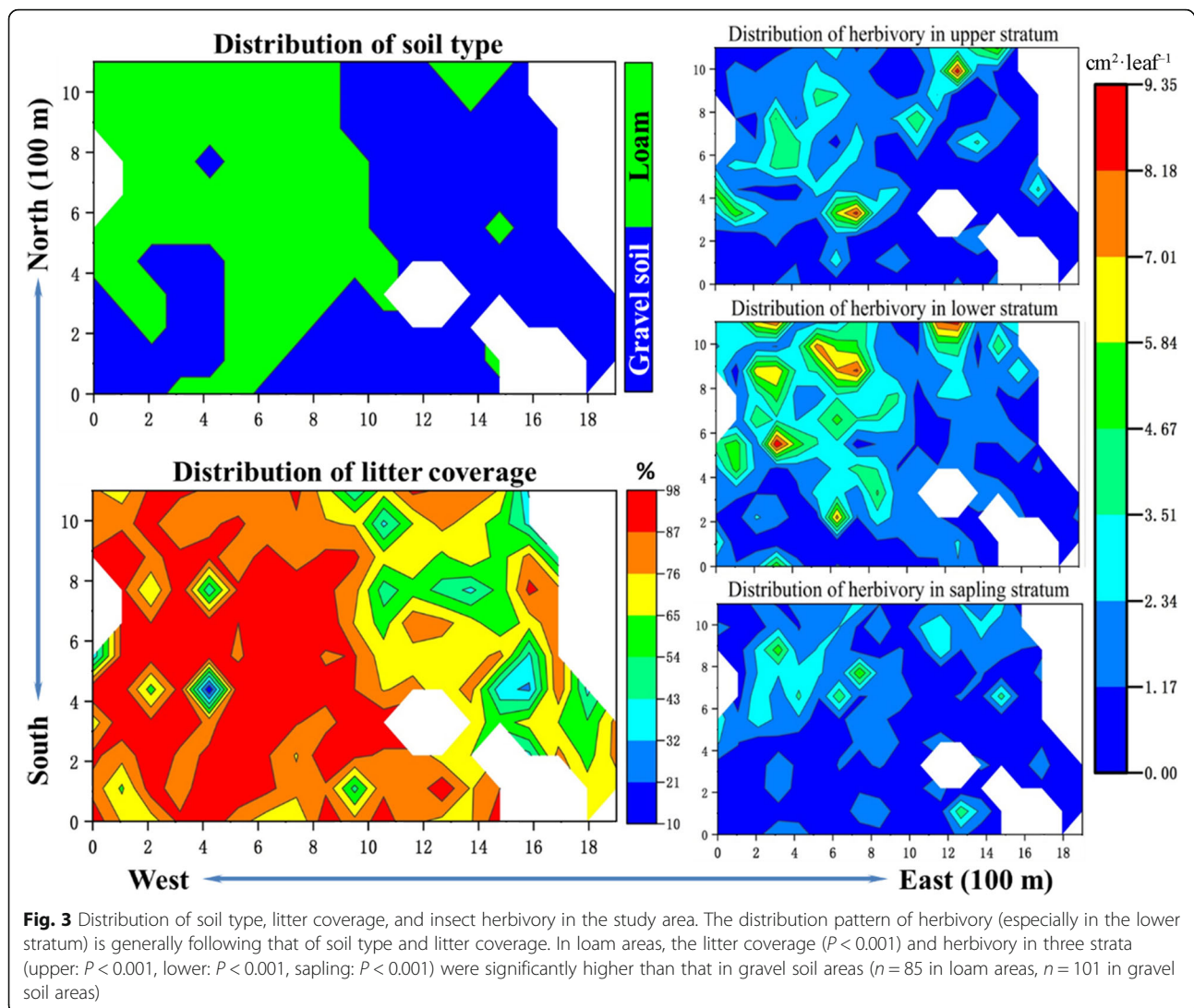
and 3). In gravel soil areas, herbivory was significantly higher in the lower stratum, but it did not differ between the upper and the sapling stratum (Figs. 2 and 3).

In contrast to the general spatial patterns across 186 plots, herbivory in some individual plots in gravel soil areas was higher than that in loam areas and there were also 41 individual plots that the highest herbivory existed in the upper stratum and 29 individual plots that the highest herbivory existed in the sapling stratum. Coverage of shrubs and herbs in these 29 plots was significantly lower than that in plots which had the highest herbivory in the upper or lower stratum (Fig. 4a). Twenty-two out of the 29 individual plots were located in the gravel soil area where the coverage of shrubs and herbs was significantly lower than that in the loam area ($n = 85$ in loam areas, $n = 101$ in gravel soil areas, $t = 5.893$, df = 184, $P < 0.001$). In the loam area, herbivory in the sapling stratum was negatively correlated with the coverage of shrubs and herbs (Fig. 4b).

Geostatistical parameters of insect herbivory are shown in Table 1. The data of herbivory in upper stratum (HU) and herbivory in sapling stratum (HS) were best fit by exponential models, the data of herbivory in lower stratum (HL) was best fit by the linear model. The $C_0/(C + C_0)$ values in our study ranged from 0.389 to 0.685, indicating moderately spatial dependence
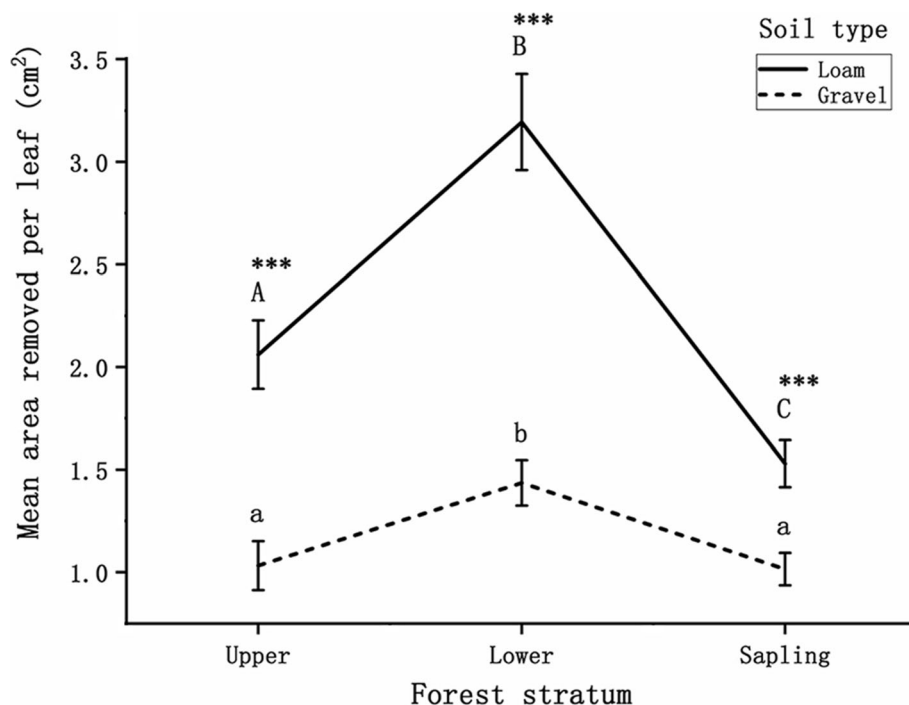
Fig. 2 Interactive effects of soil type and forest stratum on leaf herbivory (± SE, *n* = 85 in loam areas, *n* = 101 in gravel soil areas). Letters above bars indicate statistical differences between strata. The asterisk manifests a significance level between soil types in each stratum

Fig. 3 Distribution of soil type, litter coverage, and insect herbivory in the study area. The distribution pattern of herbivory (especially in the lower stratum) is generally following that of soil type and litter coverage. In loam areas, the litter coverage ($P < 0.001$) and herbivory in three strata (upper: $P < 0.001$, lower: $P < 0.001$, sapling: $P < 0.001$) were significantly higher than that in gravel soil areas ($n = 85$ in loam areas, $n = 101$ in gravel soil areas)

for insect herbivory. The A values ranged from 1,035 to 1,821 m, indicating a strongly structured regional pattern of insect herbivory.

Effects of soil conditions on insect herbivory and effects of soil type and forest stratum on leaf traits
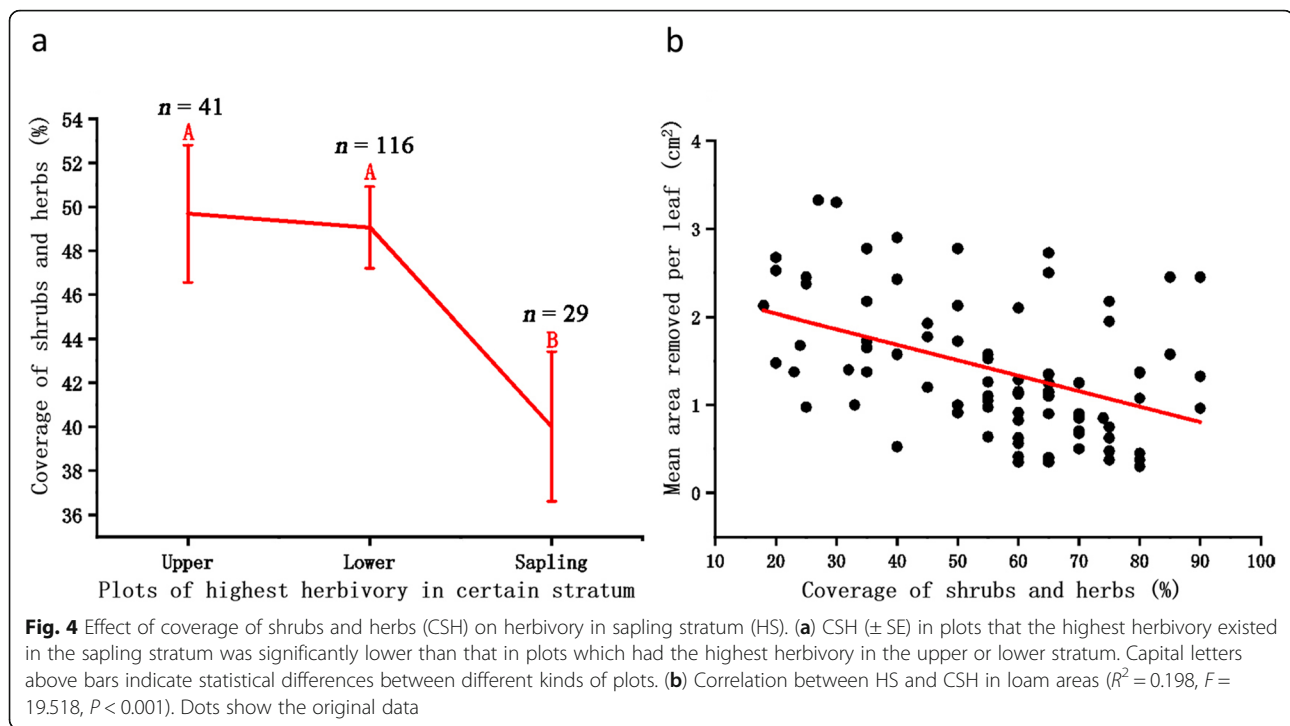
The available N and K contents and soil moisture content of loam were significantly higher than that of gravel soil, but there was no difference in available P content between loam and gravel soil (Fig. 5). Insect herbivory was positively correlated with soil moisture (Fig. 6).

Forest stratum had significant effects on SLA, soluble sugar content, tannin content, N content, and C content, but these leaf traits did not differ between soil types (Table 2). SLA decreased from the sapling stratum to the upper stratum and it was significantly lower in the upper stratum than that in the lower and sapling

stratum, but there was no difference between the lower and sapling stratum (Fig. 7). Soluble sugar content in the upper stratum was significantly higher than that in the lower and sapling stratum whereas there was no difference between the lower and sapling stratum (Fig. 7). The tannin content in the sapling stratum was significantly higher than that in the lower and upper stratum but there was no difference between the lower and upper stratum (Fig. 7). N content and C content were lower in the lower stratum than that in the upper and sapling stratum, but the differences were not significant (Fig. 7).

Density of overwintering pupae and holding effects of different soil types on withered leaves

We found 13 overwintering pupae and 37 previous pupal cases left by adults after eclosion. Ten pupae and 25 pupal cases were found in the loam area, 3 pupae and

Fig. 4 Effect of coverage of shrubs and herbs (CSH) on herbivory in sapling stratum (HS). (**a**) CSH (± SE) in plots that the highest herbivory existed in the sapling stratum was significantly lower than that in plots which had the highest herbivory in the upper or lower stratum. Capital letters above bars indicate statistical differences between different kinds of plots. (**b**) Correlation between HS and CSH in loam areas ($R^2 = 0.198$, $F = 19.518$, $P < 0.001$). Dots show the original data

12 pupae cases were found in the gravel soil area (Table 3). The density of overwintering pupae and pupal cases as well as litter coverage in the loam area were significantly higher than that in the gravel soil area (Fig. 8). All of them were found in the soil under the leaf litter. No pupae or pupal cases were found in the bare soil both in loam and gravel soil areas. The results indicated that litter is necessary for the overwintering of main insect herbivores in the study area. Higher litter coverage in loam areas may provide a better microhabitat for overwintering pupae.

The 1.5 m·s^{-1} wind did not blow away the withered leaves on both loam and gravel soil ground. When the wind speed was 2.5 and 4 m·s^{-1}, the average moved distances of withered leaves on loam ground were significantly smaller than that on gravel soil ground (Fig. 9).

Discussion

Soil type may have major effects on insect herbivory by influencing litter coverage. Soil type and litter coverage were significantly correlated with insect herbivory in three strata. Trials of holding effects showed that withered leaves fell on the gravel soil ground can be blown away easier by the wind (Fig. 9). In addition, the coverage of shrubs and herbs which can help to block and hold the leaf litter is significantly lower in gravel soil areas than that in loam areas. These may be why the litter coverage in gravel soil areas is significantly lower than that in loam areas (Fig. 3). Our survey indicated that leaf litter which provided the shelter of overwintering pupae might play an important role in the survival of main insect herbivores in the study area. The horizontal distribution pattern of herbivory (especially in the lower stratum) was generally following that of litter coverage (Fig. 3), implying the evident effects of litter coverage on insect herbivory. In geostatistical analysis, the $C_0/(C + C_0)$ values (0.389–0.685) indicated moderately spatial dependence for insect herbivory while the large spatial range (1035–1821 m) indicated a strongly structured regional pattern of insect herbivory (Liu et al. 2014). These
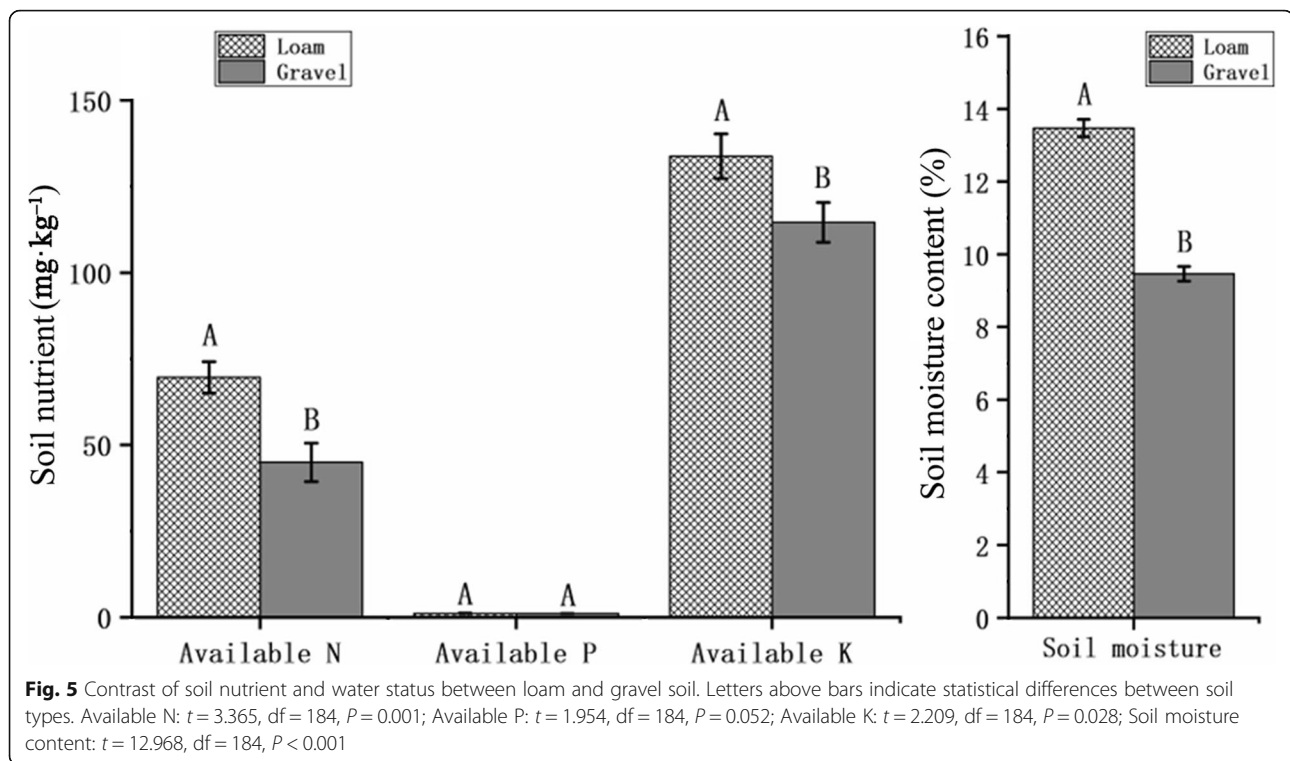
Table 1 Spatial semivariogram models and geostatistical parameters for HU, HL, HS

Variable	Model	Nugget (C_0)	Sill ($C_0 + C$)	$C_0/(C_0 + C)$	Range (A, m)	RSS	r^2
HU	exponential	0.591	1.213	0.487	1035	0.021	0.891
HL	linear	0.400	0.030	0.389	1666	0.372	0.978
HS	exponential	0.342	0.602	0.685	1821	0.344	0.912

HU Herbivory in the upper stratum; *HL* Herbivory in the lower stratum; *HS* Herbivory in the sapling stratum; *RSS* residual sum of squares;
*r^2* Determination coefficients

Fig. 5 Contrast of soil nutrient and water status between loam and gravel soil. Letters above bars indicate statistical differences between soil types. Available N: $t = 3.365$, df = 184, $P = 0.001$; Available P: $t = 1.954$, df = 184, $P = 0.052$; Available K: $t = 2.209$, df = 184, $P = 0.028$; Soil moisture content: $t = 12.968$, df = 184, $P < 0.001$

results could also imply the effects of relatively concentrated soil types and litter coverage (Fig. 3) on insect herbivory.

Leaf traits may not be the key factors influencing insect herbivory in the field. Horizontally, although the available N and K contents and soil moisture of loam were significantly higher than that of gravel soil, which is in accordance with the pattern of insect herbivory, all the leaf traits were not different between soil types. Therefore, our results do not support that the nutrient and water status of different soil types within stands can influence insect herbivory by affecting leaf traits. Vertically, many studies have suggested that the effects of environmental factors on insect herbivory that generally decreases from understory to upper stratum can be mediated by leaf traits (e.g. Stiegel et al. 2017; Castagneyrol et al. 2019). Although our pattern of increasing SLA from upper to sapling stratum coincides with previous studies (Ellsworth and Reich 1993; Koike et al. 2001; Al Afas et al. 2007; Stiegel et al. 2017; Castagneyrol et al. 2019), the vertical herbivory pattern does not (Figs. 2 and 7). The effects of forest stratum on SLA, tannin content, soluble sugar content, N content, and C content were also inconsistent with that on insect herbivory (Figs. 2 and 7). It is widely believed that unfavorable leaf traits (e.g., lower SLA, lower nitrogen content, and higher carbon content) indicate the lower leaf quality and could negatively influence leaf palatability and

consequently suppress higher herbivory (Feeny 1970; Coley et al. 1985; Reynolds and Crossley 1997; Brunt et al. 2006; Zehnder et al. 2009; Stiegel et al. 2017; Castagneyrol et al. 2019). However, studies have further demonstrated that leaf palatability or insect performance is not consistently related to insect herbivory levels in the field and to the measured leaf traits (Fortin and Mauffette 2002; Niesenbaum and Kluger 2006; Ruhnke et al. 2009; Alalouni et al. 2014). Insect herbivores can also be forced to increase their feeding rates on low-quality plants to compensate for the decline in food quality (Lincoln et al. 1993; Castagneyrol et al. 2018). This indicates that low leaf quality per se may have divergent effects on insect herbivory. The lepidopterous larva is one of the keystone "forest pests" in many temperate forests (Feeny 1970; Nothnagle and Schultz 1987; Kamata 1991). Although leaf damage is caused by the larva, transfer (usually passive) scope of the larva is limited at background herbivory level (White and Whitham 2000), patterns of herbivory are molded by a variety of factors that influence host accessibility to its female adult (Beyaert and Hilker 2014; Webster and Cardé 2017; Castagneyrol et al. 2019; Shao et al. 2019). When the food is plentiful in the field, there is no adequate evidence to support that the larvae can/need actively search for more palatable leaves within a host tree (except that newly hatched larvae may need to feed on young leaves) or more palatable host trees among different individuals for feeding. Thus, leaf traits that

Fig. 6 The correlation between insect herbivory and soil moisture. Dots show the original data
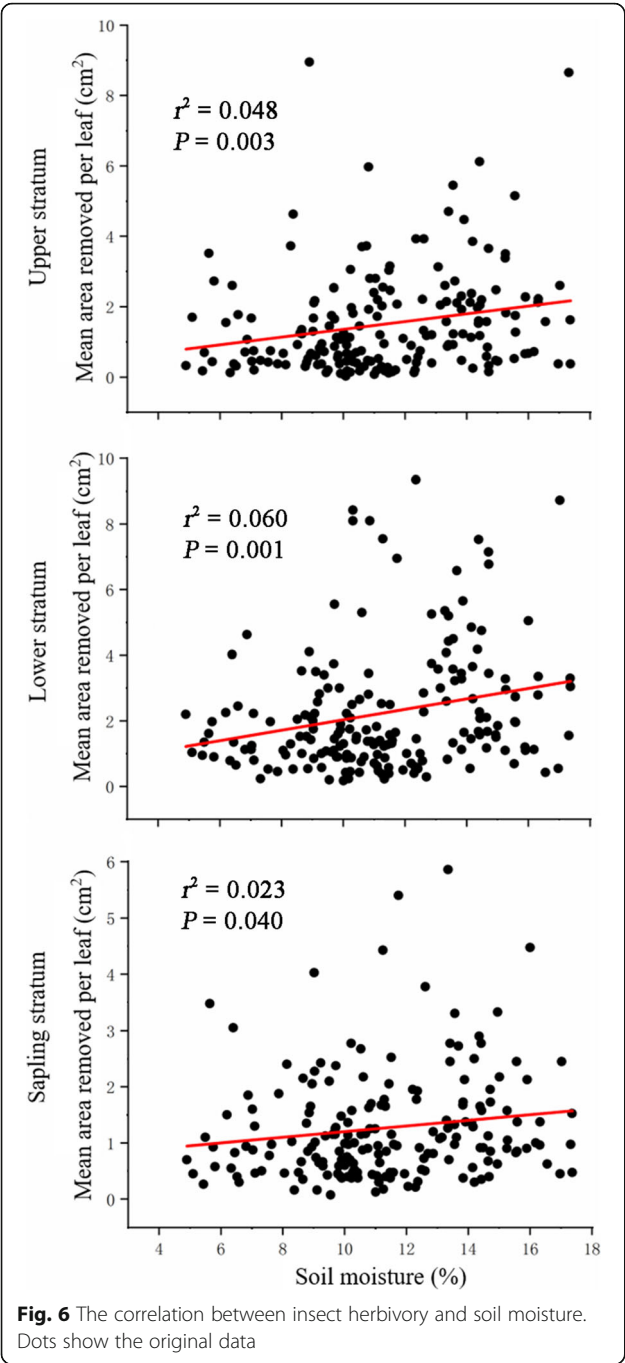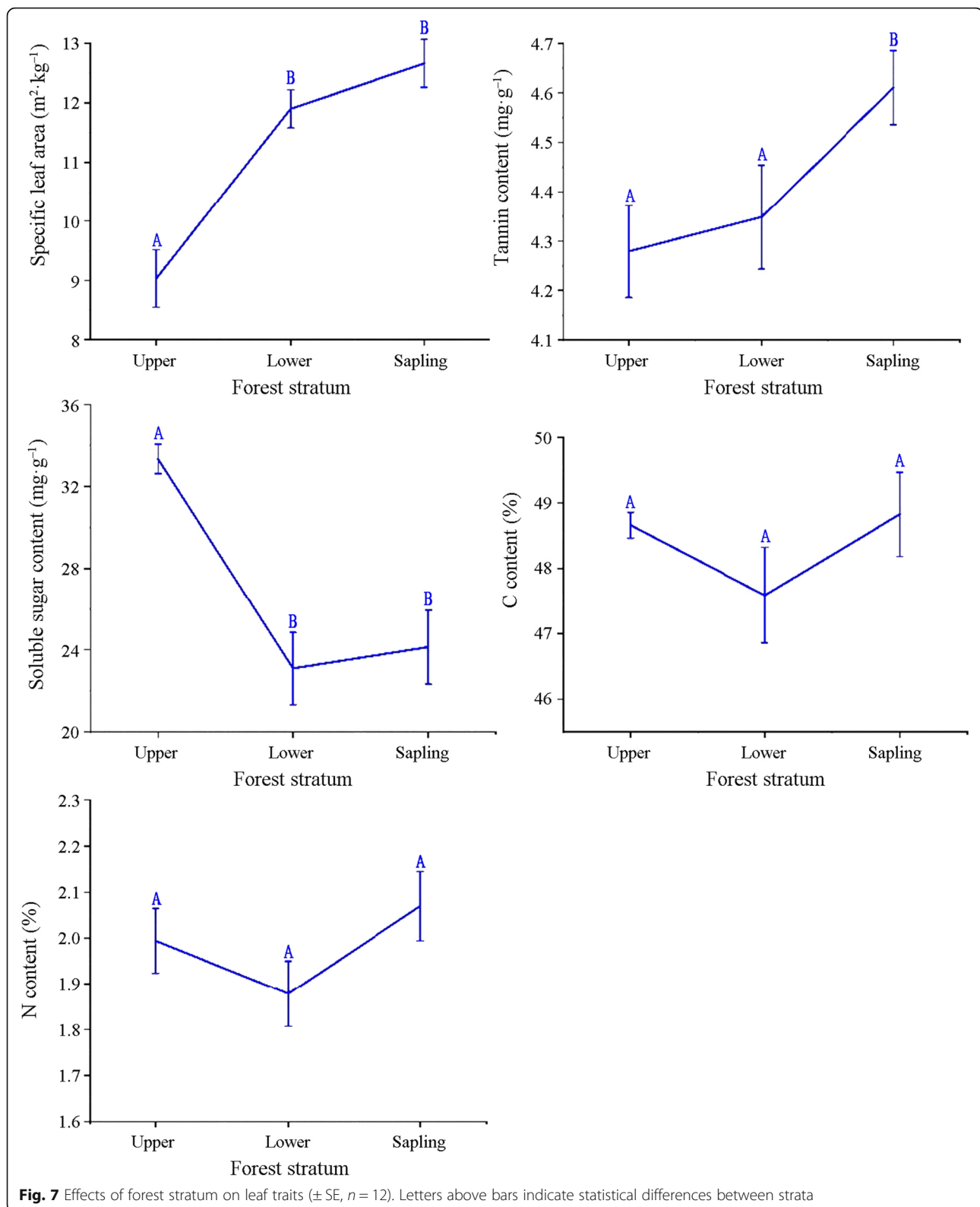
indicate leaf quality/palatability may not exert significant effects on the patterns of herbivory on a host tree species in the field.

On the other hand, entomopathogenic fungi, which can cause high mortality of overwintering insect herbivores (Kienzle et al. 2008; Kova et al. 2021), have been considered as important lethal factors of insects and thus may have significant effects on insect herbivory (Vega et al. 2009). Their growth and infection efficiency can be influenced by weather conditions (temperature and humidity) (Kienzle et al. 2008; Eilenberg et al. 2013), soil moisture (Fuxa and Richter 2004), and nutrition in the habitat (Pereira et al. 1993; Jackson et al. 2009). Our results showed that soil available N and K contents and soil moisture, as well as insect herbivory in the loam area, were significantly higher than that in the gravel soil area (Figs. 2 and 5). Insect herbivory was positively correlated with soil moisture (Fig. 6). These results imply that soil nutrient and water status may also have important effects on insect herbivory by influencing entomopathogenic fungi. However, the insect-fungus interactions that respond to soil conditions could be very complex. For example, the *Beauveria bassiana* can survive better in relatively dry soil (Lingg and Donaldson 1981; Studdert et al. 1990) but cause no difference in the mortality of *Spodoptera exigua* between different soil moistures (Studdert and Kaya 1990). Another study reported that the highest mortality of *Solenopsis invicta* Buren caused by *Beauveria bassiana* occurred at a moderate soil moisture level between "wet" and "dry" (Fuxa and Richter 2004). Thus, in our study area, the abundance and diversity of fungi in the soil, the optimum range of soil moisture and other environmental factors for the infection of fungi, and the exact contribution of entomopathogenic fungi to the spatial patterns of insect herbivory still need further examination.

The coverage of shrubs and herbs negatively influenced oak herbivory in the sapling stratum. The pattern that herbivory in the sapling stratum was significantly lower than that in the lower stratum in our study differs from other studies (e.g. Stiegel et al. 2017; Castagneyrol et al. 2019). Beyond the general herbivory pattern among strata, there were 29 individual plots that the highest

Table 2 Summary of linear mixed models testing for effects of soil type and forest stratum on leaf traits. Significant effects are indicated in bold

Predictors	SLA	Tannin content	Soluble sugar content	C content	N content
Soil type	$F_{(1, 10)} = 0.0003$ $P = 0.987$	$F_{(1, 10)} = 0.764$ $P = 0.403$	$F_{(1, 10)} = 0.456$ $P = 0.515$	$F_{(1, 30)} = 1.455$ $P = 0.239$	$F_{(1, 10)} = 3.236$ $P = 0.102$
Stratum	$F_{(2, 20)} = $ **37.102** $P < 0.001$	$F_{(2, 20)} = $ **4.399** $P = 0.026$	$F_{(2, 20)} = $ **18.532** $P < 0.001$	$F_{(2, 30)} = 1.361$ $P = 0.272$	$F_{(2, 20)} = $ **3.786** $P = 0.040$
Soil type × Stratum	$F_{(2, 20)} = 1.184$ $P = 0.327$	$F_{(2, 20)} = 0.217$ $P = 0.807$	$F_{(2, 20)} = 1.258$ $P = 0.306$	$F_{(2, 30)} = 0.741$ $P = 0.485$	$F_{(2, 20)} = 0.887$ $P = 0.427$

Fig. 7 Effects of forest stratum on leaf traits (± SE, *n* = 12). Letters above bars indicate statistical differences between strata

herbivory existed in the sapling stratum. The coverage of shrubs and herbs in these plots was significantly lower than that in other plots (Fig. 4a). In the loam area,

herbivory in the sapling stratum was negatively correlated with the coverage of shrubs and herbs (Fig. 4b). Previous studies have demonstrated that greater herbivore species
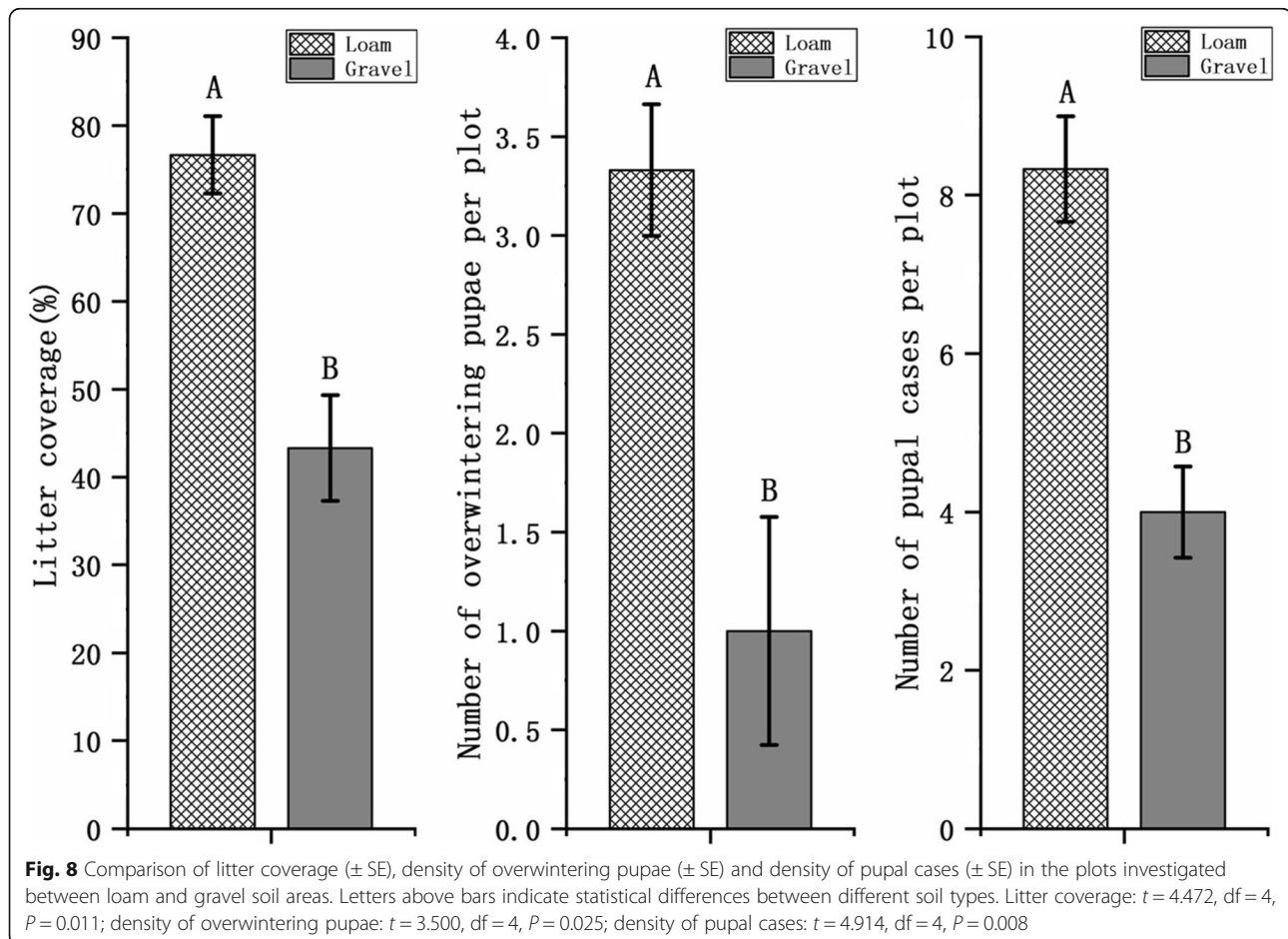
Table 3 The litter coverage, number of overwintering pupae, and pupal cases in each plot
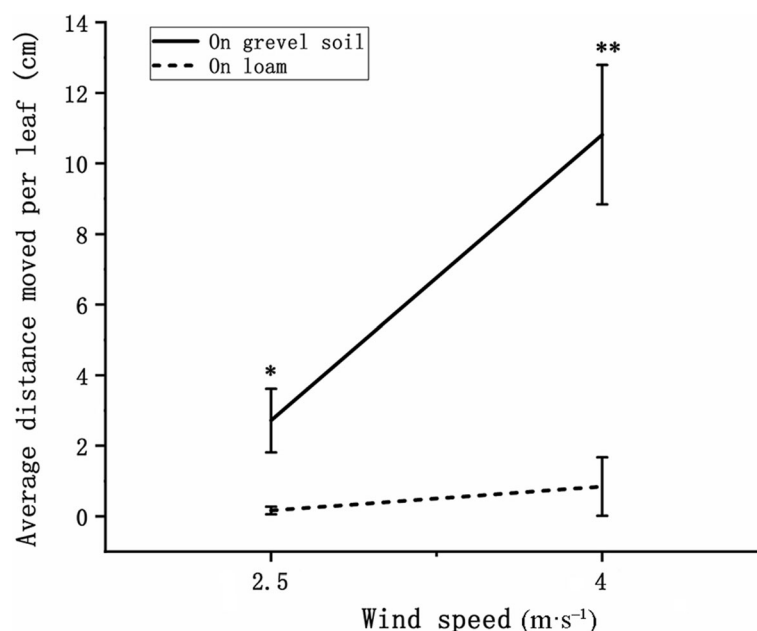
Parameters	Loam area			Gravel soil area		
	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
Litter coverage (%)	70	85	75	40	35	55
Overwintering pupae	3	3	4	0	1	2
Pupal cases	7	9	9	4	3	5

richness and abundance may occur on the plants that offer larger resources (Bach 1980; Evans 1983; Marques et al. 2000; Barbosa et al. 2009; Leidinger et al. 2019). The identity and diversity of surrounding plants can also influence herbivory on host plants by altering the physical and chemical apparency of focal plants (Finch and Collier 2000; Castagneyrol et al. 2013; Moreira et al. 2016). In this study area, the range of *Quercus variabilis* Bl. sapling height was 10 to 150 cm while many shrubs grew more than 200 cm. The biomass of saplings is "tiny" relative to their adults and most of the saplings are surrounded by grasses and shrubs, which can decrease the physical and chemical apparency of the oak saplings, which may be why the herbivory in sapling stratum is significantly lower than that in lower stratum.

Conclusions

Insect herbivory was spatially heterogeneous within stands. In general, herbivory was significantly lower in gravel soil areas than in loam soil areas. The highest herbivory occurred in the lower stratum, the lowest in the sapling stratum. However, there were also 41 individual plots in which the highest herbivory occurred in the upper stratum and 29 plots in which the highest herbivory occurred in the sapling stratum. There were significant differences in soil nutrient and water status between soil types, but differences in leaf traits were not significant. The effects of the forest stratum on leaf traits were inconsistent with those on insect herbivory. Leaf traits may not be the main factors influencing insect herbivory in the field. Soil type may have a prominent effect

Fig. 8 Comparison of litter coverage (± SE), density of overwintering pupae (± SE) and density of pupal cases (± SE) in the plots investigated between loam and gravel soil areas. Letters above bars indicate statistical differences between different soil types. Litter coverage: $t = 4.472$, df = 4, $P = 0.011$; density of overwintering pupae: $t = 3.500$, df = 4, $P = 0.025$; density of pupal cases: $t = 4.914$, df = 4, $P = 0.008$

Fig. 9 Holding effects of loam and gravel soil on withered leaves. The smaller the average distance moved per leaf (± SE, $n = 6$) the stronger the holding effect. The asterisk manifests a significant level between soil types in each wind speed (2.5 m·s^{-1}: $P = 0.036$; 4 m·s^{-1}: $P = 0.003$)

on herbivory patterns due to changes in litter composition while higher coverage of shrubs and herbs may reduce herbivory in the sapling stratum. These findings contribute significantly to our understanding of tree-herbivore interactions in real-world situations and thus have important implications for the sustainable management of forest ecosystems.

Authors' contributions
Xinliang Shao, Qin Zhang and Xitian Yang conducted the conception, design of the work, data collection, statistical analysis, draft of the work. The authors read and approved the final manuscript.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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